

## NATURAL AND INDUCED DIFFERENCES IN PROBING BEHAVIOR OF TWO BIOTYPES OF THE GREENBUG, *SCHIZAPHIS GRAMINUM*, IN RELATION TO RESISTANCE IN SORGHUM

CLYTIA B. MONTLLOR<sup>1),2)</sup>, BRUCE C. CAMPBELL<sup>2)</sup> and T. E. MITTLER<sup>1)</sup>

<sup>1)</sup> Department of Entomological Sciences, University of California, Berkeley, CA 94720 and <sup>2)</sup> USDA, ARS, Western Regional Research Center, Berkeley, CA 94710, U.S.A.

A recently discovered biotype of the greenbug, *Schizaphis graminum* (Rondani), biotype E (GBE), was found to grow and reproduce at approximately twice the rate of biotype C (GBC) on a GBC-resistant variety of sorghum, IS 809. The probing behavior of both biotypes was electronically monitored on IS 809. Aphids of GBE established committed phloem ingestion (CPI) (i.e., ingestion from the phloem lasting > 15 min) in a significantly shorter amount of time than did aphids of GBC. The total duration of phloem ingestion during a 24 hr period was significantly longer for GBE than for GBC, but this can be partially accounted for by the shorter time needed for aphids of GBE to establish initial CPI. Once CPI was initiated, aphids of both biotypes tended to ingest for long periods (> 8 hr) from the phloem of IS 809 during the 24 hr assay. Further experiments showed that GBC exposed to IS 809 for at least 24 hr prior to being monitored on this variety also reached the phloem faster, established CPI sooner, and spent longer feeding from the phloem than did GBC without previous exposure to this variety. The significance of these findings towards an understanding of the mechanism of resistance of IS 809 to GBC and to the breakdown of this resistance to GBE is discussed.

**KEY WORDS:** Greenbug — *Schizaphis graminum* — *Sorghum bicolor* — Host-plant resistance — Aphid biotypes — Conditioning — Electronic monitoring.

Biotypes are often morphologically indistinguishable and are usually designated on the basis of a difference in some biological character, such as insecticide resistance or host-plant preference (Eastop, 1973). Many aphid biotypes, in particular, have been discovered by their appearance on new or previously resistant host-plant species or varieties, suggesting a change in feeding preference and/or behavior. Using an electronic device to monitor aphid probing behavior, Nielson & Don (1974) measured several characteristics of this behavior in 4 biotypes of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), on clones of alfalfa which differed in resistance to the biotypes. When any given biotype fed on an alfalfa clone that was resistant to it, there was little or no ingestion from the phloem, whereas biotypes feeding on their respective susceptible clones ingested for significantly longer periods from the phloem.

Saxena & Chada (1971) examined the differ-

ences in the location in plant tissue of stylets of two biotypes of the greenbug, *Schizaphis graminum*, feeding on wheat. They found that the stylets of one biotype (biotype A) chiefly terminated in the phloem while the stylets of the other biotype (biotype B) most often terminated in mesophyll parenchyma. Campbell *et al.* (1982) examined the probing behavior of a third biotype of the greenbug, biotype C (GBC), on resistant and susceptible varieties of sorghum, *Sorghum bicolor* L. (Moench). GBC fed for significantly less time from the phloem of the resistant varieties compared to the susceptible varieties tested. Based on these observations, it was suggested that phloem chemistry may be an important factor in explaining sorghum resistance to GBC. Other studies of feeding behavior have also revealed a correlation between a lack of or greatly reduced ingestion from the phloem and aphids probing resistant host-plants (Kennedy *et al.*, 1978) or nonhost plants (McLean & Kinsey, 1968; Nault & Styer, 1972; Campbell *et al.*, 1982). Other aspects of monitoring of aphid feeding behavior in relation to host-plant differences are reviewed by Tarn & Adams (1982).

In 1980 a new biotype of the greenbug was discovered in the field in Bushland, Texas. This new biotype was shown to damage GBC-resistant varieties of wheat and sorghum and was designated biotype E (GBE) (Porter *et al.*, 1982). In order to investigate whether the natural breakdown of resistance (measured here by aphid growth and fecundity) to this biotype may have come about by a change in the aphids' probing behavior, we compared certain electronically monitored behavioral characteristics of biotypes C and E feeding on a GBC-resistant variety of sorghum (IS 809). We also investigated induction of behavioral changes in GBC aphids resulting from previous exposure to the resistant host-plant, since plant background is known to affect settling, feeding, and reproductive behavior of aphids (McLean, 1971; Lowe, 1973).

#### MATERIALS AND METHODS

Adult apterous virginoparae from stock laboratory cultures of *S. graminum*, maintained in growth chambers (18–20°, 16L : 8D), were used for all probing assays, as well as for development and fecundity assays. Aphids of GBC were maintained on barley seedlings unless noted otherwise. Aphids of GBE, originally obtained from Dr. S. D. Kindler (University of Nebraska, Lincoln) in 1981, were maintained on sorghum seedlings of IS 809 or on barley seedlings. Each biotype culture was derived from a single aphid.

**Fecundity and development.** The fecundity of each biotype was measured by placing single 1-day-old adult aphids on 2-wk-old seedlings of IS 809. This assay was replicated 12 times for each biotype. Larvae deposited by each adult were counted and removed every 2–3 days, and the adults transferred to fresh seedlings, weekly, as long as they continued to larviposit. After larviposition ceased, the aphids were no longer transferred, but were kept on the same plants until the aphids died. One cohort of larvae of each biotype, born in a 24 hr period 1 wk after the beginning of the experiment, was allowed to grow to adulthood, at which time each aphid was individually weighed.

**Probing behavior.** Probing behavior was electronically monitored as previously described for GBC (Campbell *et al.*, 1982). Aphids were tethered with a gold wire and placed on the ad-axial surface of the first or second fully ex-

panded leaf of the test plant within 5 min of removal from the culture. All test plants for the first 3 of 4 experiments were 6- to 8-wk-old sorghum of the GBC-resistant variety IS 809, grown in the greenhouse. For the fourth experiment the GBC-susceptible variety of sorghum BOK-8, grown under the same conditions, was also used. Probing behavior was monitored at room temperature under constant light for 24 hr (Exps. I–III) or until the phloem was reached (Exp. IV). All assays began with the initiation of the first probe.

**Exp. I** — This experiment compared probing behaviors of GBE and GBC monitored on IS 809 when aphids of each biotype were raised on different culture plants. GBE aphids were reared on IS 809 seedlings; GBC aphids were reared on barley and transferred to the susceptible sorghum variety BOK-8 for 1–5 days prior to monitoring.

**Exp. II** — This experiment was similar to Exp. I except that GBC and GBE aphids were both reared on the same culture plant, barley. One aphid of GBC and one of GBE were monitored simultaneously on the same leaf of each IS 809 test plant.

**Exp. III** — The probing behavior of two cohorts of GBC aphids was compared on IS 809. In one cohort, young adult aphids were transferred from their culture plant to clip-cages on IS 809 for 1–3 days prior to monitoring ("conditioned"), while aphids of the other cohort were transferred to clip-cages on BOK-8 for the same amount of time ("unconditioned"). Two GBC aphids, one conditioned and the other not, were monitored simultaneously on the the same leaf of each test plant of IS 809.

The following probing phenomena relating to penetration of and ingestion from the phloem were measured in Exps. I–III (waveforms generated by the electronic monitoring of greenbug probing activities are described by Campbell *et al.*, 1982): 1) the length of time elapsed before aphids reached the phloem with their stylets, measured as minutes from initial plant penetration to production of the first X-wave (diagnostic for penetration of a phloem sieve tube), 2) the time taken to establish committed phloem ingestion (CPI), measured as minutes to the first X-wave followed by > 15 min of ingestion from the phloem (in our experience, an aphid which ingested from the phloem continuously for at least 15 min tended to remain feeding in phloem for up to several

hours), 3) the total number of X-waves produced during 24 hr, 4) the total number of separate probes (i.e., stylets withdrawn and re-inserted into plant tissue) made during 24 hr, and 5) the number of separate probes and amount of phloem ingestion (measured as percent of the remaining assay time spent ingesting from the phloem) that occurred *after* the initiation of the first CPI. In Exp. I, 15 aphids of GBC and 16 of GBE were monitored; 17 aphids of each biotype were monitored in Exp. II; and 10 aphids of GBC from each treatment were monitored in Exp. III.

Exp. IV — In order to test whether an aphid would reach the phloem more quickly if it were forced to probe repeatedly on the same leaf, GBC and GBE (raised on BOK-8 and IS 809, respectively) were monitored on resistant and susceptible sorghums in the following way: An aphid of each biotype was tethered and the two aphids were placed on the same leaf of the test plant (either BOK-8 or IS 809) for simultaneous recording of probing behavior. Each aphid was allowed to make a series of probes until it produced an initial X-wave. Its feeding was then disrupted and the aphid was moved to a different part of the same leaf (a new "feeding site") and allowed to probe until it produced another X-wave. This procedure was repeated 1–4 times for 7 aphids of each biotype on 7 IS 809 plants and 5 aphids of each biotype on 5 plants of BOK-8. Each time an aphid was placed at a new feeding site several successive probes were usually made before a probe resulting in an X-wave was established. At each feeding site, the interval between the initiation of the first of these successive probes to the production of an X-wave was measured, as was the time between the initiation of the last of these successive probes (i.e., the probe containing the X-wave) and the occurrence of the X-wave.

All probing data from the 24 hr assays were analyzed non-parametrically, using either the Mann-Whitney U statistic (Wilcoxon rank sum test) for unpaired samples (Exps. I) or the Wil-

coxon signed rank test for paired samples (Exps. II and III). Data from Exp. IV were analyzed by ANOVA.

## RESULTS

*Fecundity and development.* These results are summarized in Table I. Aphids of GBE were significantly more fecund compared to GBC when both were reared on IS 809 seedlings. During the first week of adulthood, the mean number of larvae deposited/♀/day was similar for the two biotypes; however, the rate of larviposition of GBC declined sharply after the first 5 days. GBE aphids deposited larvae for approximately 1 wk longer, on average, than GBC aphids. GBE also had a longer post-reproductive life-span than GBC. Finally, GBE aphids reared from birth on IS 809 seedlings took less time to develop into adults than GBC and weighed significantly more as adults than those of GBC on IS 809.

*Probing behavior.* The results of Exps. I–III are summarized in Table II.

Exp. I — Aphids of GBE took significantly less time than aphids of GBC to reach the phloem with their stylets (min to 1st X-wave) when feeding on IS 809. GBE took less than half as long, on average, as GBC to establish CPI. GBE also fed from the phloem for significantly longer, made significantly fewer separate probes, and made significantly fewer X-waves than did GBC aphids during the 24 hr assay. The proportion of remaining time spent ingesting from the phloem after the initiation of the first CPI was also significantly greater for GBE compared to GBC. However, the number of probes made after the initiation of CPI was not significantly different for the two biotypes.

Exp. II — In this experiment, comparing the two biotypes reared on the same host-plant, barley, all measured probing characteristics were significantly different between GBC and GBE except for the time to the first X-wave.

TABLE I

*Means of reproductive parameters of two greenbug biotypes (GBC and GBE) larvipositing on sorghum variety IS 809; mean weights and development times from birth to 5th instar (adult) for the two greenbug biotypes born on IS 809. \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  (ANOVA)*

Biotype	No. larvae/adult	Reproductive lifespan (days)	Post-reproductive lifespan (days)	Adult wt. (μg)	Days to Adulthood
GBC	37.8	27.6	7.1	164.1	11.2
GBE	71.7***	35.2**	22.5**	308.5***	9.5***

TABLE II

Means of electronically monitored probing activities of greenbug biotypes GBC and GBE with given plant background, when feeding on sorghum variety IS 809 (Exps. I—III) calculated for the entire 24 hr assay period and/or after the initiation of the first CPI (committed phloem ingestion).

Biotype/ pl. backgr.	Min to 1st X-wave	Min to 1st CPI	During 24 hr Assay		After 1st CPI		
			Total phloem ingestion (min)	No. probes	No. X-waves	No. probes	% phloem ingestion
Exp. I							
GBC/BOK-8	361.9	529.3	689.1	31.0	8.5	9.0	71.8
GBE/IS 809	192.9**	242.3**	997.4**	16.2*	4.6*	5.9 ns	86.7*
Exp. II							
GBC/barley	189.7	549.0	527.3	47.8	11.2	20.2	59.8
GBE/barley	152.3 ns	231.0**	1022.5**	14.2**	5.7**	5.1*	79.4*
Exp. III							
GBC/BOK-8	306.1	488.0	398.1	59.3	9.6		
GBC/IS 809	132.7*	288.1*	828.2**	32.3**	9.3 ns		

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; ns, not significant ( $P > 0.05$ )

GBE look less than half as long to establish CPI and ingested from the phloem for approximately twice as long as did GBC. GBE also made fewer separate probes and fewer X-waves in 24 hr than did GBC. In addition, GBE made fewer probes after the first CPI was established, and the proportion of post-CPI phloem ingestion was significantly greater for GBE than for GBC.

In Exps. I and II almost half of the GBC

monitored (14/32) fed for a total of  $> 10$  hr from the phloem of IS 809 over the 24 hr assay period. All of the GBE aphids of Exps. I and II fed for  $> 8$  hr from the phloem, and all but 2 of the 33 GBE aphids tested fed for  $> 10$  hr in the phloem of IS 809 (Fig. 1).

Exp. III — All probing events measured in this experiment were significantly different for conditioned (exposed to IS 809) compared to unconditioned GBC aphids, except for the

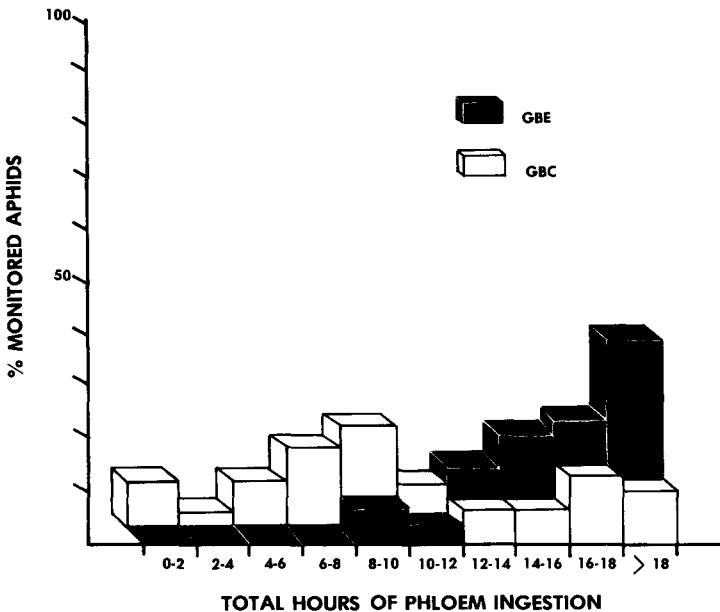


Fig. 1. Percentage of aphids of each greenbug biotype (GBC and GBE) feeding for given number of hours (total ingestion during a 24 hr period) from the phloem of IS 809 sorghum. (Based on calculations made from recordings of all GBC and GBE greenbugs monitored in Exps. I and II.)

number of X-waves produced. Conditioned aphids reached the phloem and established CPI sooner than their unconditioned counterparts. Conditioned aphids also fed from the phloem for longer and made fewer probes than unconditioned aphids.

Exp. IV — The results of the comparison between GBC and GBE sequentially probing new feeding sites on BOK-8 and IS 809 sorghum are summarized in Table III. There was no significant difference between the time period from the first probe to production of an X-wave at the first feeding site (i.e., at the first site the aphid was placed after tethering) for a given aphid compared to the average of subsequent periods for the same aphid at new feeding sites on the same leaf. These data (initial probe to X-wave) were therefore pooled for each aphid biotype. This period was significantly shorter for GBE than for GBC feeding on IS 809. There was no significant difference in this interval between the biotypes when probing the susceptible BOK-8. Finally, it took GBC aphids significantly less time to produce an X-wave when probing BOK-8 compared to IS 809.

The time from the initiation of the last probe at each feeding site to the production of the X-wave at that site was not significantly different between GBC and GBE on either IS 809 or BOK-8 (Table III). The only significant difference in this probing characteristic was between GBE probing BOK-8 compared to either biotype probing IS 809. The average duration of the last probe terminating in an X-wave was similar for GBE and GBC on IS 809.

## DISCUSSION

The significantly longer time spent feeding from the phloem, greater absolute fecundity, increased longevity, longer post-reproductive life, more rapid development and larger size of

GBE compared to GBC when monitored or reared on IS 809 sorghum indicate that this variety, while retaining its resistance to GBC, is relatively more susceptible to GBE. Previous research showed that IS 809 was resistant to GBC based on studies of plant damage, and aphid growth and reproduction on IS 809 compared to other, susceptible, varieties (Weibel *et al.*, 1972; Schuster & Starks, 1973; Campbell *et al.*, 1982). Our results show that the feeding behavior, reproduction and growth of GBE on IS 809 is comparable to that shown for GBC on GBC-susceptible varieties of sorghum. IS 809 is a variety of *S. bicolor*, originating in India (Schuster & Starks, 1973), whereas the varieties of GBC-resistant sorghums tested against GBE by Porter *et al.* (1982) derive their resistance from *S. virgatum* (Hack.) Stapf, originating in Egypt (De Wet & Huckabay, 1967). It is interesting that GBE has overcome the resistance in sorghum from both of these distinct genetic sources.

Campbell *et al.* (1982) proposed that differences in chemical constituents of the phloem between resistant and susceptible varieties of sorghum might account for the differential feeding behavior of GBC on these varieties. The production of defensive chemicals ("phytoalexins") by resistant host-plants in response to penetration of the sieve tubes by aphid stylets (Nielson & Don, 1974; Kennedy *et al.*, 1978) has also been suggested. However, we have found that, after a number of successive probes, GBC will ingest for long periods from the phloem of the resistant IS 809, suggesting that GBC aphids can adjust to the presence of a feeding deterrent, or the absence of a feeding stimulant, which may characterize the resistant host-plant. In preliminary studies (Montllor, unpublished observations), 3 compounds which are known to be feeding deterrents to GBC (i.e., p-hydroxybenzaldehyde, p-hydroxy-

TABLE III

*Means of two electronically monitored probing parameters of greenbug biotypes GBC and GBE feeding on GBC-resistant (IS 809) and susceptible (BOK-8) sorghum (Exp. IV). Means followed by different letters within columns are significantly different ( $P < 0.05$ )*

Biotype/plant background	Plant monitored	Initial probe to 1st X-wave (min)	Final probe to X-wave (min)
GBE/IS 809	BOK-8	84.7 a	26.9 a
	IS 809	97.3 a	41.3 b
GBC/BOK-8	BOK-8	113.9 a	36.0 ab
	IS 809	201.4 b	43.1 b

benzoic acid, and dhurrin, Dreyer *et al.*, (1981) were equally deterrent to both biotypes when incorporated into artificial diets. Therefore, it seems unlikely that any of these compounds play a role as feeding deterrents in the phloem of IS 809 to which GBC is more sensitive than GBE. We cannot rule out the existence of other feeding cues (e.g., stimulants) peculiar to IS 809 to which GBE may be more sensitive than GBC, or which GBC may be able to more rapidly discern or respond to after a period of conditioning.

The relatively longer time taken by GBC, compared to GBE, to reach and ingest from the phloem of IS 809 plants may be an important factor in explaining the resistance of this variety, since the magnitude of the difference in total duration of phloem ingestion between the two biotypes may be due in large part to the longer time GBC takes to establish CPI compared to GBE. Aphids of both biotypes can reach the phloem within 45 min of inserting their stylets into leaf tissue. However, these rapid stylet insertions to the phloem are almost invariably preceded by many separate probes which include salivation and non-phloem ingestion, and which account for the much longer time taken by GBC aphids to make an X-wave (reach the phloem) each time they are moved to a new feeding site on IS 809 compared to GBE. These numerous probes may be an important part of the behavioral repertoire of an aphid, by which it gathers the necessary information to determine whether it is on an acceptable plant. In addition, hydrolysis of plant tissues by salivary enzymes during repeated probes in the same leaf area may facilitate eventual stylet penetration to the phloem. Therefore, non-phloem factors may play an important role in the resistance of IS 809 to GBC. Despite the apparent conditioning of GBC aphids, this process may have to be repeated periodically by the aphids during the course of their development on IS 809. If so, then the additive effect of such long pre-CPI periods, possibly equivalent to intermittent periods of fasting, could have a considerable impact on the growth and reproduction of GBC aphids. Auclair & Cartier (1960) found that when *Acyrtosiphon pisum*, maintained on a susceptible variety of pea, were fasted for 8–12 hr a day for several days their growth and reproduction was equivalent to that of aphids reared on resistant varieties of peas.

Differences in the probing behavior, growth,

and reproduction of the two aphid biotypes on sorghum are assumed to be genetically based. However, short-term behavioral and/or physiological adaptations must be invoked to account for the induced changes in relative acceptability of IS 809 to conditioned GBC aphids. It is likely that most aphids engage in repeated exploratory probes before settling down for prolonged feeding on an acceptable plant (see Pollard, 1973 for a review of aphid feeding). On less suitable host-plants, pre-CPI probing may be very extensive, and on non-hosts, phloem ingestion may never occur. The conditioning phenomenon reported here for GBC indicates that modifications in aphid probing behavior may be made as a result of exposure to a "new" host-plant. Effects of past experience on behavior are known for many insects (e.g., Prokopy *et al.*, 1982; Saxena & Schoonhoven, 1982 and references therein). For aphids, they have been observed in relation to starvation (McLean & Kinsey, 1969), and to culture and/or previous feeding experience on plants or artificial diets (McLean, 1971; Lowe, 1973). Confinement to a relatively unacceptable host-plant may lead to partial starvation or to sensory adaptation, either of which might be expected to lower the acceptance threshold of the aphids. The capability for such behavioral modifications may represent a necessary step in the process of genetic adaptation of the sort that GBE shows on IS 809, since behaviorally, the only difference between GBC and GBE aphids is the rapidity with which they are able to feed efficiently on IS 809 (and, likely, other resistant sorghum varieties). Short-term physiological adaptation (e.g., changes in activity of salivary enzymes) of aphids raised on plants in different physiological conditions (Adams, 1967) may also be involved in the apparent conditioning of aphids.

Because we found no significant differences between the growth or reproduction of GBC aphids reared on barley and assayed on IS 809 and that of GBC aphids both reared and assayed on IS 809 (Montllor and Mittler, unpublished observations), we conclude that the changes in probing behavior made by GBC as a result of previous exposure to IS 809 are not reflected in the long-term performance of GBC on this variety. Therefore, it is not clear whether the biotype differences in probing behavior exhibited in Exps. I and II are directly responsible for the differential growth and fe-

cundity of GBC and GBE on IS 809. Possible reasons for the lack of correspondence between probing behavior of conditioned GBC aphids and their long-term performance on IS 809 include: 1) there is a constituent in the phloem sap of IS 809 that is detrimental to the growth and fecundity of GBC but not to GBE, 2) GBE is more efficient than GBC at using the nutritional resources in the IS 809 plant, or 3) a 24 hr assay of the feeding behavior of these aphids does not give a representative view of their long-term feeding behavior. Both the phenomena of adaptation by GBE to this previously greenbug-resistant variety of sorghum and of "conditioning" of GBC to IS 809 need further investigation.

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#### ZUSAMMENFASSUNG

#### Natürliche und induzierte Unterschiede im Probiervverhalten zweier Biotypen von *Schizaphis graminum*

Wachstum und Fortpflanzung beim kürzlich entdeckten Biotyp E (GBE) von *Schizaphis graminum* (Rondani) war ungefähr zweimal grösser als bei Biotyp C (GBC) und zwar auf der GBC-resistenten Sorghumsorte IS 809. Das Stechverhalten beider Biotypen wurde auf IS 809 elektronisch verfolgt. GBE-Läuse begannen erheblich schneller mit der ununterbrochenen Saftaufnahme (dh Saftaufnahme, die mehr als 15 Minuten anhielt) als GBC-Läuse. Die Gesamtzeit der Saftaufnahme innerhalb 24 Stunden war bei GBE erheblich länger als bei GBC. Dies ist zum Teil darauf zurückzuführen, dass die GBE-Läuse weniger Zeit brauchten, um mit der ununterbrochenen Saftaufnahme zu beginnen. Wenn diese einmal begonnen hatte, nahmen beide Biotypen gewöhnlich während langer Perioden (über 8 Stunden) Saft von IS 809 auf. Weitere Experimente zeigten, dass GBC-Läuse, die mindestens 24 Stunden vor der Beobachtungszeit Zugang zu IS 809 gehabt hatten, Saft schneller fanden, ununterbrochene Saftaufnahme früher begannen und die Saftaufnahme länger fortsetzten als GBC, die vorher nicht Zugang zu dieser Sorte gehabt hatten. Die Bedeutung dieser Beobachtungen für das Verständnis des Resistenzmechanismus von IS 809 gegen GBC und des Zusammen-

sammenbruchs dieser Resistenz gegen GBE wird besprochen.

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